TAXONOMIC NOTES ON THE GENERA *STENOTIS* AND *CARTERELLA* (RUBIACEAE) AND TRANSFER OF *HEDYOTIS GREENEI* TO *STENOTIS*

Edward E. Terrell

Research Associate
Department of Botany, MRC 166
Smithsonian Institution
Washington, D.C. 20013-7012, U.S.A.
Terr60@msn.com

Harold Robinson

Curator
Department of Botany, MRC 166
Smithsonian Institution
Washington, D.C. 20013-7012, U.S.A.
Robinsoh@si.edu

ABSTRACT

A limited review of the genus *Stenotis* (Hedyotidae/Spermacoceae: Rubiaceae) is provided using morphological characters. The circumscription of the genus *Stenotis* is expanded with **Hedyotis greenei** A. Gray transferred to the genus. The genus *Carterella*, evidently closely related to *Stenotis* on the basis of some structures, geography, cytological data, and recent molecular phylogenetic study, is considered as generically distinct.

RESUMEN

Los limites del género *Stenotis* (Hedyotideae/Spermacoceae: Rubiaceae) se discuten, **Hedyotis greenei** se transfiere al género. *Carterella* que se considera como un género estrechamente vinculado pero distinto.

The genus *Stenotis* Terrell (2001) includes seven species restricted to Baja California and Arizona, two annuals and five perennial herbs or small shrubs. The present study is a reconsideration of taxonomic relationships in the genus. Five of the species have chromosome numbers of $n = 13$ (Lewis 1962a), a number so far known only in *Stenotis* and *Carterella* Terrell in the *Hedyotis* L./*Houstonia* L. relationship. A study by Church (2003), using nuclear and chloroplast DNA sequences, included two species of *Stenotis*, *S. arenaria* and *S. asperuloides*, and the single species, *Carterella*, and concluded that they were closely related to each other but in a phylogenetic position outside of the *Houstonia* L./ *Stenaria* Terrell clade. The *Stenotis* clade remains most distinct in its $n = 13$ chromosome number, and its near restriction to Baja California.

In our previous studies of *Hedyotis/Houstonia* relationship, we have emphasized the taxonomic importance of seed morphology. In the case of *Stenotis* the seeds of all species have punctiform hila on or near the middle of the seeds. The annual species differ somewhat from the perennials in having the ventral, hilar face somewhat enlarged and rounded (Table 1). Seeds of four species were shown by Terrell (2001, Fig. 1).

COMPARISON OF SPECIES

The present study is an addendum to the monograph of *Stenotis* by Terrell (2001), and a key to the species is contained in that study. Six of the seven species of *Stenotis* are considered here. The present study does not deal with *S. peninsularis* (Brandegee) Terrell, a very rare, twice-collected species. Of the remaining species, we propose, based on our investigation, that one species in the previous treatment (Terrell 2001) is of hybrid origin and *Hedyotis greenei* (A. Gray) W.H. Lewis be transferred from *Hedyotis* into *Stenotis* as discussed below. a probable older name for the previously recognized *Stenotis arenaria* (Rose) Terrell.

Within *Stenotis*, the type species *S. mucronata*, is distinguished from all other species by having fasciculate morphology, described as follows: Stem densely branched and with many short internodes, leaves often sessile, unusually small, 3–18 × to ca. 2 mm, numerous, linear or subterete, thick and rigid, strongly revolute, tightly clustered at the nodes in groups of 3–8 or more. This combination of characters gives the plants a densely unique appearance. At least several species of *Arcytophyllum* Willd. ex Schult. in Roem. & Schult., a related South and Central American genus, have similar fasciculate morphology; the relationships of these species to *Stenotis* has not been tested, and is the subject of a separate study.

TABLE 1. It is not possible to include *Stenotis greenei* in this table, which was provided at the time of the monograph to compare the established species of the genus. It can be noted here that *S. greenei* is closely related to *S. arenaria*, but the extent of this closeness remains to be determined. If the two prove conspecific, the name *S. greenei* would have priority.

	mucronata	**brevipes**	**australis**	**arenaria**	**asperuloides**
HABIT	small shrubs/ herbs	small shrubs/ herbs	per. woody herbs	small annual herbs	small annual herbs
STEMS	to 9 dm tall	to ca. 1 m.	to 6 dm tall	0.3–3.0 dm tall	to 2.8 dm tall
texture	woody, stout	herb./woody base	woody toward base	herbaceous	herbaceous
branching	dense	spreading	spreading	spreading	diffusely branched
vestiture	glabrate or glabrous	glabrous	glabrous/puber.	glabrous/scaber.	glabrous/ puber.
LEAVES L × W	3–18 × to 1.8 mm	5–30(–50) × 0.3–2	to 40 × to 2	5–40 × 0.5–6.0	3–30 × 0.3–3.5
shape	linear/subterete	linear or filiform	linear or filiform	narr.oblanc.to linear	linear or filiform
fasciculate	densely	not fasciculate	not fasciculate	not fasciculate	not fasciculate
texture	thick, rigid	herbaceous	herbaceous	herbaceous, thin	herbaceous
apex	mucronulate	apiculate/mucronul.	obtuse to apiculate	acute to apiculate	obtuse to apiculate
PEDICELS/SESSILE	subsess./ped. to 10 mm	subsess./ped. to 12	sessile/ped. to 10	sessile/ped. to 16	sessile/ped. to 30
COROLLAS L. mm	8–14	8–18	4–11	2–6	3–11
shape	tubular	tubular	tubular	short-tubular	short-tubular
tubes mm	7–10	6–13	3–7	1–3.5	2–7
lobes	1.5–4.0 × 1–3	1.5–5.0 × 1–3	1.5–3.5 × 1–2	1–3 × 0.5–2.0	1.5–5.0 × 1–4
lobes/tubes	tubes. 3–4 × longer	tubes 3–4 × longer	tubes 2 × longer	equal	tubes sl. longer
vesture	glabrate	glabrous	glab/puber. within	glabrous	puberulent
CAPSULES mm	1.7–3.5 × 2–3.5	1.5–3.5 × 1.5–3.5	2–4 × 2–4	2–4 × 2–4	1.3–5.0 × 1.3–2.0
shape	subglobose	subglobose	subglobose	subglobose/ obovoid	turbinate/ obl/ell
l/w	equal/sl.wider than long	equal	equal	equal	longer than wide
SEEDS	0.65–0.95 × 0.35–0.6	0.6–1.0 × 0.3–0.7	0.45–0.8 × 0.3–0.6	0.4–0.9 × 0.25–0.60	0.3–0.6 × 0.2–0.4
compression	moderate	moderate/strong	moderate	slight	slight/ moderate
thickness	moderate	moderate	moderate	thick	thick
outline shape	ellipsoid/oblongoid	broadly ellipsoid	oblongoid/irregular	obl./ell./irreg.angul.	ell./obl.
ventral face	flat/concave	concave/sl. convex	flat/sl. convex	str.convex, rounded	str.convex, rounded
hilum	centric punctiform hilum	centric punct. hilum	centric punct. hilum	centric punct. hilum	centric punct. hilum

In spite of the fasciculate morphology in *Stenotis mucronata* (Benth.) Terrell, three perennial species are clearly rather closely related. *Stenotis mucronata* has woody, stout stems to ca. 9 dm tall. The perennial species most similar to *S. mucronata is S. brevipes* (Rose) Terrell, which has herbaceous stems to ca. 1 m tall. *Stenotis brevipes* does not have fasciculate morphology and the herbaceous leaves are 5–50 mm long. When the two species are compared in detail (Table 1), we find that, aside from the fasciculate morphology, they are generally similar in calyx, corolla, capsules, and seeds.

A third perennial species, *S. australis* (I.M. Johnst.) Terrell, is somewhat smaller, ca. 6 dm tall, with stems woody toward the base (Table 1). It differs from *S. brevipes* mainly in having corollas somewhat shorter and corolla tubes 2 times longer than the lobes instead of 3–4 times longer. *Stenotis australis* has a more restricted

range south of La Paz in lower Baja California, whereas *S. brevipes* is rather widely distributed northward. Terrell (2001) examined 13 herbarium specimens of *S. australis*, and 41 collections of *S. brevipes*.

The two annual species, *S. arenaria* (Rose) Terrell and *S. asperuloides* (Benth.) Terrell, occur in the Cape region of Baja California south of La Paz. Both have short, slender herbaceous stems. When the two species are compared with each other (Table 1) they differ as follows: Leaves slightly larger in *S. arenaria* and narrowly oblanceolate to linear compared to linear or filiform in *S. asperuloides*. Pedicels in *S. arenaria* are to 16 mm long, compared to 30 in *S. asperuloides*. Corollas in *S. arenaria* 2–6 mm long vs. 3–11 mm. Corolla tubes and lobes about equal in *S. arenaria*, but slightly longer in *S. asperuloides*. Capsules equally long and wide in *S. arenaria*, but slightly longer than wide in *S. asperuloides*. Capsule shape in *S. arenaria* often subglobose but often turbinate in *S. asperuloides*. Seeds are similar in both species. We conclude that the two annual species have several differences, but are similar in important characters such as seeds.

Comparison of the annual *S. arenaria* with the perennial species having herbaceous stems, *S. brevipes* (Table 1), shows differences besides those of plant size and life cycle: *S. arenaria* has corollas only 2–6 mm long and corolla tubes about equal in length to the lobes, but *S. brevipes* has corollas 8–18 mm long with tubes 3–4 times longer than lobes. Seeds of *S. arenaria* are slightly compressed and thick with the ventral face strongly rounded. Seeds of *S. brevipes* are moderately compressed with both similar faces concave or convex. These differences in reproductive characters suggest that these two species are more distantly related.

The other annual species, *S. asperuloides*, may also be compared (Table 1) with *S. brevipes*. *Stenotis asperuloides* has pedicels to 30 mm long, corollas 3–11 mm long and corolla tubes only slightly longer than the lobes. *Stenotis brevipes* has pedicels to 12 mm long, corollas 8–18 mm long, and tubes 3–4 times longer than the lobes. The capsules of *S. asperuloides* are often turbinate and the length of capsules is longer than its width. The capsules of *S. brevipes* are often subglobose and equally long as wide. Seeds of *S. asperuloides* and *S. brevipes* differ as in *S. arenaria* and *S. brevipes*.

It was noted above that all three perennial species are closely related to each other in spite of the occurrence of fasciculate morphology in *S. mucronata*. The two annual species appear to be basically similar to each other in important characters such as seeds, but in other characters they are distinct. It is concluded that the annual and perennial species appear to be rather distinct groups, but are correctly placed in the same genus, especially as no other genus except *Carterella* appears to be related to *Stenotis*.

Status of *Stenotis gracilenta*

Johnston (1924) described *Houstonia gracilenta* and noted it resembled both *H. brevipes* and *H. mucronata*, "particularly the latter." Wiggins (1980) stated that *H. gracilenta* occurred on several islands in the Gulf of California. Both of the species that Johnston compared with his new species are well known to occur on these islands, and there is at least one collection of *S. mucronata* from San Diego Island (*Moran 9592*, MICH), the type locality for *S. gracilenta* (Terrell 2001).

Stenotis gracilenta was tentatively treated as a species by Terrell (2001), who accompanied it with nomenclatural data and a full description, but suggested that it is likely to be a hybrid between *S. brevipes* and *S. mucronata*. Terrell (2001) provided a description to *S. gracilenta* and included it in the key to species. The evidence from the intermediate structure and co-occurrence with putative parents is sufficient to confirm its hybrid status. It may be listed as *Stenotis* × *gracilenta* (I.M. Johnston) Terrell.

Transfer of Hedyotis greenii to genus Stenotis

Terrell (2001) stated that an additional species, *Hedyotis greenei* A. Gray, occurs only in Arizona and is closely related to *Stenotis arenaria*, or the same species, but it was excluded from his treatment pending further study. Since 2001 Terrell has not found time or opportunity for further study, however, data strongly suggest that *Hedyotis greenei* is a *Stenotis*. It will take other studies to determine whether it is truly distinct from the very morphologically similar *Stenotis arenaria*, but they are clearly both members of *Stenotis*. Whether it is distinct from *S. arenaria* or is the same species or a variety remains to be determined. The geographical separation of the two taxa—lower Baja California and Arizona amounts to ca. 960 km (600 miles). It may be noted that

the name *S. greenei* (1883) predates the name *S. arenaria* (Rose 1890). It is not possible to properly include *Stenotis greenei* in Table 1, which was provided to compare the established species; it is pointed out here that *S. greenei* is closely related to *S. arenaria*, but the extent of this closeness remains to be determined.

Stenotis greenei (A. Gray) Terrell & H. Rob., comb. nov. *Oldenlandia greenei* A. Gray, Proc. Acad. Arts 19:77.1883. *Hedyotis greenei* (A. Gray) W.H. Lewis, Rhodora 63:222.1961. *Houstonia greenei* (A. Gray) Terrell, Phytologia 59:79.1985. TYPE: U.S.A. NEW MEXICO: Pinos Altos Mountains, 1880, *E.L. Greene 149* (HOLOTYPE GH!). PARATYPE: ARIZONA: Ramsey's Canyon, S. Arizona, 1882, *Lemmon 2719* (GH!, attached to the same sheet with the type).

Small annual herb with slender roots. Stems 3–16 cm tall, slender, quadrangulate to terete, erect, glabrous or scabridulous, with slender branches 2–10 cm long from any or all nodes. Leaves 5–32 × 0.5–5.0 mm, sessile or with short petioles, thin, 1-nerved, narrowly oblanceolate, narrowly elliptic, or linear, glabrous. Stipules to 1 mm long, scarious, whitish, with several marginal teeth. Inflorescence with heterostylous flowers, earliest flowers sessile in axils of peduncles or branches, surpassed by later peduncles bearing sessile or pedicellate flowers. Pedicels to ca. 16 mm long, erect, buds obovate. Hypanthium glabrous; calyx lobes 0.5–2.0 × 0.2–0.7 mm, lanceolate or narrowly lanceolate. Corollas 2–5.5 mm long, funnelform, white; tubes 1–3.5 mm long, 0.5–1.5 mm wide at throat, glabrous within; lobes 1–2 × 0.5–2 mm, ovate. Pin flowers with stigma lobes 0.2–0.5 mm long, linear, exserted to ca.1 mm long beyond throat, anthers at or just below corolla throat. Thrum flowers with anthers 0.2–0.4 mm long, oblong, subsessile or on filaments to 1 mm long, exserted to ca. 1 mm beyond throat, stigmas near midpoint of tube. Capsules 2–4 mm long and wide, ¾–⅞ inferior, subglobose, tan with 8 darker nerves, thin-walled, dehiscing loculicidally and septicidally. Seeds 0.5–0.8 × 0.3–0.45 mm, brown, oblong or elliptic, dorsal face flattish or convex, ventral face strongly rounded with punctiform apical hilum, testa reticulate, areole (cell) walls sinuous or straight. Chromosome number not known.

Phenology.—Flowering August–September; fruiting September–October.

Habitats and distribution.—Gravelly soil, on boulders or bedrock outcroppings, rocky slopes; pine-oak forests, oak-juniper; 1500–2450 m (5000–8000 ft). Southeastern and central Arizona (Cochise, Graham, Greenlee, Pima, Santa Cruz, Yavapai counties), southwestern New Mexico.

Additional nomenclatural notes.—Gray's protologue listed two collections. The first was *E.L. Greene 149* from New Mexico (see above). This citation was set off by a period and space and was followed by citation of "S. Arizona, in Ramsey's Cañon, 1882, *Lemmon.*" We take it that the first citation is a holotype (not a syntype) as it was distinctly set off and the name of the collector, Greene, was used in the species name. The second name is a paratype, not a syntype, as it was not equal in status to the first name.

Representative Specimens. **ARIZONA. Cochise Co.:** Blacktail Canyon, Fort Huachuca Military Reservation, *Goodding 390-61* (ARIZ); pine-oak forest, 6200 ft, Rucker Canyon, Chiricahua Mts., *Gould & Haskell 4551* (ARIZ); Huachuca Mts., Miller Canyon road, 2.3 mi W of Hwy. 92, *McLaughlin & Hoffman 5242* (ARIZ). **Graham Co.:** near Chlarsons Mill, Pinaleno Mts., 6500 ft, *Shreve 4376* (ARIZ). **Pima Co.:** Rincon Mts., 7900 ft, Manning Camp, *Blumer 3369* (ARIZ, DS, ISC, MO); near top of Mt. Baboquivari, 7500 ft, *Gould 4475* (ARIZ, CAS). **Santa Cruz Co.:** Madera Canyon, *Fletcher 2836* (UNM). **Yavapai Co.:** Prescott Pines Baptist Campground, *Keil 712* (ASU).

Relationships of the genus *Carterella*

The genus *Carterella* was established by Terrell (1987) based on *Bouvardia alexanderae*, a rare Baja.California species named by Annetta Carter in honor of her friend, Annie M. Alexander, for her assistance in a 1949 trip to Baja California. Annetta Carter was impressed by the "large white long-tubed salverform corollas" so assigned the species to *Bouvardia* (Carter 1955). Lewis (1962b) found that *Bouvardia alexanderae* has a chromosome number of $n = 13$, the same as the number for other Baja California species (Lewis 1962a) that are now placed in *Stenotis*. Later, Lewis (1968) transferred the species to *Hedyotis* L., using the broad interpretation of the genus that was in use at that time. Terrell and Robinson (2003) reported that *Hedyotis fruticosa* L., the type species, was related to a number of Asian species morphologically distinct from American species, consequently we restrict use of the name *Hedyotis* to Asian taxa.

Terrell (1987) renamed *Carterella* as a monotypic genus, discussed the morphology, and considered it distinct from *Hedyotis*. Church (2003) in molecular studies stated that the chloroplast data place *C. alex-*

anderae firmly within the *Stenotis* lineage. A question at the present time is whether *Carterella* (1987) and *Stenotis* (2001) are the same genus. Here the evidence is reexamined. Because *Carterella* is in an unresolved or basal position in the *Stenotis* clade (Church 2003), we suggest the lineage includes two genera, one being the monophyletic *Carterella*.

Carterella alexanderae is a narrowly restricted endemic confined to granitic canyons in the mountains east and southeast of La Paz in lower Baja California. It is quite different from the species of *Stenotis* discussed here, and is a conspicuously attractive species with flower parts two to several times longer or larger than those of *Stenotis* (Terrell 1987, Fig. 1). Its calyx lobes are 3–10 mm long versus 0.5–3 in *Stenotis* species; corollas are 30–50 mm long versus 2–18; corolla tubes 25–41 mm long versus 1–13; corolla lobes 4.5–10 mm long versus 1–5; anthers 1.8–3 mm long versus 1–1.7; and stigma lobes 1–5 mm long versus 1–1.8. In fruit the capsules length and width are 3–6 × 3–6 mm versus 1.3–5 × 1.3–4, significantly larger than most if not all previously studied taxa in the Hedyotideae (s.s.). These measurements indicate that the length and width of important flower and fruit characters are quantitatively different in *Carterella*.

Our previous work on the Hedyotideae (s.s.) found that seed morphology provided significant evidence concerning the taxonomic status of genera and species. In studying *Carterella alexanderae* we found this again to be true. Seeds of *Carterella alexanderae* are strongly to moderately, laterally compressed with a hilum at the peak (Terrell 1987, Figs. 2, 3) whereas seeds of *Stenotis* are somewhat dorsiventrally compressed, of an ellipsoid type with a punctiform hilum on or near the center of the ventral face. *Carterella alexanderae* is considered to be unique in having this strong lateral compression. Previous studies have not shown species of *Hedyotis/Houstonia* relationship with such extreme morphology. Here it may also be noted that *Bouvardia* seeds are dorsiventrally compressed with wide, papery, conspicuous wings and a chromosome number of 9.

Terrell (1987) stated that *Carterella alexanderae* "appears to be an offshoot or derivative of the same basic stock as that of the *Houstonia mucronata* group" (now *Stenotis*), perhaps long isolated and the result of considerable differentiation. This is shown by the striking quantitative differences in flower and fruit characters and the strong qualitative differentiation in seed morphology. We believe that *Carterella* should remain a monotypic genus.

ACKNOWLEDGEMENTS

We thank Joseph Kirkbride for assistance with vagaries of computer procedure. We also thank the curators of the cited herbaria for loans during past years and reviewers of the manuscript for providing helpful assistance. Carlos Garcia-Robledo, Postdoctoral Fellow in the Department of Botany, is thanked for the Spanish resumen. We thank David Lorence and an anonymous reviewer for helpful comments on an earlier draft.

REFERENCES

Carter, A. 1955. A new species of *Bouvardia* (Rubiaceae) from Baja California, Mexico. Madrono 13:140–144.

Church, S.A. 2003. Molecular phylogenetics of *Houstonia* (Rubiaceae): descending aneuploidy and breeding system evolution in the radiation of the lineage across North America. Molec. Phylogen. Evol. 27:223–238.

Johnston, I.M.1924. Expedition of the California Academy of Sciences to the Gulf of California in 1921. Proc. Calif. Acad. Sci., ser. 4, 12:1173–1177.

Lewis, W.H. 1962a. Phylogenetic study of *Hedyotis* (Rubiaceae) in North America. Amer. J. Bot.49:855–865.

Lewis, W.H. 1962b. Chromosome numbers in North American Rubiaceae. Brittonia 14:285–290.

Lewis, W.H. 1968. Notes on *Hedyotis* (Rubiaceae) in North America. Ann. Missouri Bot. Gard. 55:31–33.

Terrell, E.E. 1987. *Carterella* (Rubiaceae), new genus from Baja California, Mexico. Brittonia 39:248–252.

Terrell, E.E. 2001. *Stenotis* (Rubiaceae), a new segregate genus from Baja California, Mexico. Sida 19:899–911.

Terrell, E.E. and H. Robinson. 2003. Survey of Asian and Pacific species of *Hedyotis* and *Exallage* (Rubiaceae) with nomenclatural notes on *Hedyotis* types. Taxon 52:775–782.

Wiggins, I.L. 1980. Flora of Baja California. Stanford University Press, Stanford, CA.